

each surface of a lipid bilayer like that proposed by Gorter and Grendel. Specifically, each protein is attached to the outward-facing head of one of the phospholipid molecules. This model offered a ready explanation for the appearance of membranes as pairs of dark lines with a lighter region between them in electron micrographs and was generally accepted for more than thirty-five years before being replaced by a model in which proteins were embedded in the membrane.

Mitochondria (1890–1925)

Discussions of mitochondria frequently attribute their discovery to the investigations of Richard Altmann around 1890.¹⁸ He introduced improved fixation techniques (e.g., a solution of potassium dichromate and osmium tetroxide). When used with an acid-fuchsin stain differentiated by picric acid, and with delicate heating, he was able to observe filaments in the cytoplasm of nearly all cell types. Although some of the structures Altmann saw were undoubtedly mitochondria, he positioned his discussion in a very different context than modern thinking about cell organelles. He titled his 1890 book *Die Elementarorganismen und ihre Beziehungen zu den Zellen* (*The Elementary Organisms and their Relations to the Cells*). His endeavor was to revise and revive the view that living substances were comprised of elementary living granules (the filaments were, for him, strings of granules). The revisions were designed to make the granular theory compatible with cell theory, and specifically with Virchow's dictum *omnis cellula e cellula*, which he then extended to granules with the dictum *omne granulum e granulo*.

In espousing the view that granules were the basic living unit, Altmann opposed the view that protoplasm has a uniform structure. He attributes basic metabolic processes (specifically, fat metabolism and secretion) to these granules. Moreover, he claimed granules were equivalent to independently existing microorganisms and named them both *bioblasts*: Because both granules and microorganisms “represent the elementary organisms which are found wherever vital forces become active we shall name them with the joint term Bioblasts. **It seems that with the bioblast [the] morphological unit of living matter has been found**” (Altmann, 1890, from an unpublished

¹⁸ This is not to say that Altmann was the first to see mitochondria. Starting around 1850 Kölliker studied granules in muscle cells. In 1888, he separated them from insect muscle and found that they swelled in water and possessed a membrane. These were probably mitochondria, but it is often very difficult to know for sure what structures (or artifacts) he and other early observers were actually observing.